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MEDITERRANEAN MARINE DEMERSAL RESOURCES: THE MEDITS INTERNATIONAL TRAWL SURVEY (1994-1999).
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Cephalopod assemblages caught by trawling along the Iberian Peninsula Mediterranean coast*

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SUMMARY: The cephalopod fauna collected in five MEDITS-ES trawl surveys carried out on the Iberian Mediterranean coast was analysed. Hauls, which were carried out in spring between 1994 and 1998, numbered 480. A total of 34 cephalopod species, grouped in 11 families, was found at depths of between 25 and 786 m. Species and samples assemblages were analysed with the Bray-Curtis similarity index. From the physical parameters studied (depth, temperature and bottom type) only depth showed a positive correlation with cephalopod distribution. Three main cephalopod communities were defined: the shelf community (< 150 m), the middle slope community (> 480 m) and a group of cephalopods which were widely distributed more abundantly on the lower continental shelf-upper slope (150-480 m). SIMPER analysis revealed that *Loligo (Alloteuthis) media* was the main indicator species of the shelf group, *Eledone cirrhosa* was the indicator species of the lower shelf upper slope group and *Todarodes sagittatus* of the middle slope community. The 150-480 m stratum was considered a transitional zone, representing an overlapping region for shelf and slope faunas.

Key words: demersal cephalopods, faunal assemblages, bathymetry, North-western Mediterranean.

INTRODUCTION

Cephalopods are a well known mollusc group in the Mediterranean, as can be seen from the literature on this taxonomic group (Naef, 1921-1923; Borri, 1986; Mangold and Boletzky, 1988; Bello, 1986). Their geographic and bathymetric distributions have been studied in detail in different areas: North Tyrrhenian Sea (Belcari *et al.*, 1986; Belcari and Sartor, 1993); Catalan Sea (Mangold-Wirz, 1963); North Tyrrhenian Sea and Catalan Sea (Sánchez *et al.*, 1998); Aegean Sea (D'Onghia *et al.*, 1996); Sicilian Channel (Jereb and Ragonese, 1986; Ragonese *et al.* 1992); Adriatic Sea (Bello, 1990; Pastorelli *et al.*, 1995); Ligurian Sea (Relini and Orsi Relini, 1984); Ionian Sea (Tursi and D'Onghia, 1992); the coasts of Libya and Tunisia (Bonnet, 1973); Marmara Sea (Katagan *et al.*, 1993); North-western Mediterranean Sea (Sartor *et al.*, 1998); and the Eastern Mediterranean Sea (Ruby and Knudsen, 1972). Regarding the Spanish Mediterranean, the most studied area is the Catalan Sea (Sánchez, 1986; Villanueva, 1992; Sánchez *et al.*, 1998, among others). The teuthofauna of the whole Iberian Peninsula has been revised by Guerra (1992), with data on the biology and distribution of the species. However, this study constitutes the first attempt to analyse the bathymetric distribution of cephalopods throughout Iberian Mediterranean waters. The aim of the present study is also to analyse the relationship between various environmental factors (e.g. depth, bottom type and temperature) and the

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cephalopod distribution on the Iberian Peninsula Mediterranean coast (NW Mediterranean). This was carried out in order to provide information concerning certain aspects, such as environmental conditions and bathymetric family diversification and how they relate to bathymetric distribution.

MATERIALS AND METHODS

A total of 480 bottom trawls was carried out in spring from 1994 to 1998, between the Strait of Gibraltar and Cape Creus (Fig. 1), at depths from 25 to 786 m. All hauls were carried out during daylight hours using the GOC 73 gear (Bertrand *et al*., 2000). To increase the catch of demersal species, this gear has a vertical opening slightly larger than the most common professional gears used in the area. The R/V "Cornide de Saavedra" was used in all surveys.

The sampling stations were distributed by applying a stratified sampling scheme with a simple random pattern inside each stratum. The stratification parameter adopted was depth, with the following bathymetric limits: 10, 50, 100, 200, 500 and 800 m. The proposed average sampling rate was one station per 60 square nautical miles. The duration of the hauls was fixed to 30 minutes at depths of less than 200 m and to 1 hour at greater depths. Details on the sampling gear (e.g. feature and handling), the design of the survey, the information collected and the management of the data by common standard analyses are described by Bertrand *et al*. (2000, 2002).

The cephalopod catch at each station was sorted, identified, and their number and biomass estimated on board. In the present study cephalopod catches were standardised to 1-hour haul duration. The generic classification of the family Loliginidae of Vecchione *et al*. (1998) was adopted.

The species composition of each haul was quantitatively analysed from a numerical matrix of every cruise separately. The Bray-Curtis measurement of similarity was used and the group average clustering method was applied in order to form dendrograms. Species which appeared only once in each survey were omitted from the analysis, since it was considered that the inclusion of such species could introduce biases in the analysis. The hauls in which only one cephalopod species appeared were consequently also removed from the analyses. All the analyses and calculations were carried out using the computer software package PRIMER (Plymouth Routines In Multivariate Ecological Research) developed at the Plymouth Marine Laboratory, United Kingdom, for the study of community structure (Clarke and Warwick, 1994), from an analytical protocol pro-

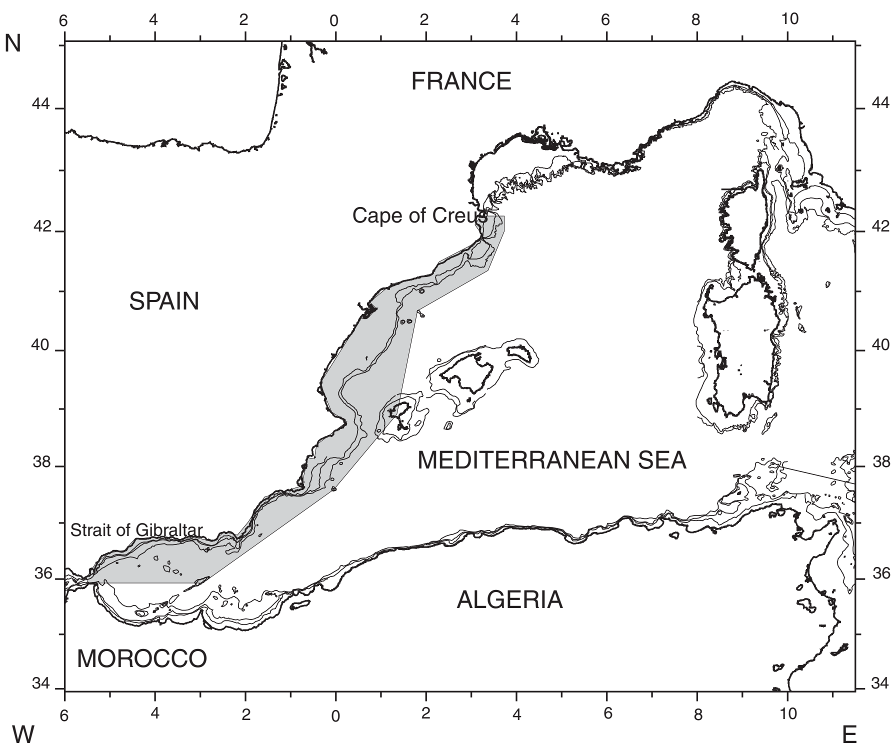

FIG. 1. – Map of the Western Mediterranean illustrating the study area.

TABLE 1. – Cephalopod species captured from 1994 to 1998 off the Iberian Peninsula Mediterranean coast (NW Mediterranean) showing their depth range, their mean depth of occurrence, with the associated standard deviation.

	MIN	MAX	MEAN	SD
Order Sepioidea				
Family Sepiidae				
Sepia officinalis Linnaeus, 1758	25	134	48.3	23.1
Sepia elegans Blainville, 1827	27	278	86.7	50.3
Sepia orbignyana Férussac, 1826	58	314	136.7	57.5
Family Sepiolidae				
Rossia macrosoma (Chiaie, 1830)	115	550	300.5	125.6
Neorossia caroli (Joubin, 1902)	47	744	429.3	162.1
Heteroteuthis dispar (Rüppell, 1844)	290	720	515.3	156.5
Rondeletiola minor (Naef, 1912)	41	616	219.4	125.7
Sepiola robusta Naef, 1912	47	81	59.2	14.4
Sepiola ligulata Naef, 1912	80	80	80.0	-
Sepiola intermedia Naef, 1912	34	82	54.6	11.8
Sepietta oweniana (Orbigny, 1840)	27	761	237.2	149.4
Sepietta obscura Naef 1916	27	56	40.5	15.6
Sepietta neglecta Naef 1916	41	113	74.0	23.0
Order Teuthoidea				
Family Loliginidae				
Loligo vulgaris Lamarck, 1798	27	317	65.5	55.0
Loligo (Alloteuthis) media (Linnaeus, 1758)	25	478	94.7	52.1
Loligo (Alloteuthis) subulata (Lamarck, 1798)	34	278	110.8	59.8
Family Chtenopterygidae				
Chtenopteryx sicula (Vérany, 1851)	725	725		
Family Enoploteuthidae				
Abralia veranyi (Rüppell, 1844)	47	761	369.5	156.8
Family Onychoteuthidae				
Onychoteuthis banksii (Leach, 1817)	650	650	650	-
Ancistroteuthis lichtensteinii (Férussac and Orbigny, 1839)	175	776	559.8	161.7
Family Histioteuthidae				
Histioteuthis bonnellii (Férussac, 1834)	451	725	578.5	88.1
Histioteuthis reversa (Verrill, 1880)	424	720	573.6	87.6
Family Brachioteuthidae				
Brachioteuthis riisei (Steenstrup, 1882)	415	725	520.0	114.1
Family Ommastrephidae				
Illex coindetii (Vérany, 1839)	46	629	144.2	112.4
Todaropsis eblanae (Ball, 1841)	44	693	278.2	158.0
Todarodes sagittatus (Lamarck, 1798)	87	786	483.5	169.8
Order Octopoda				
Family Opisthoteuthidae				
Opisthoteuthis agassizii Verrill,1883	687	795	741.0	62.3
Family Octopodidae				
Octopus vulgaris Cuvier, 1797	25	188	83.9	35.6
Octopus salutii Vérany, 1836	82	577	299.8	121.0
Scaergus unicirrhus (Delle Chiaje, 1830)	71	309	174.6	73.9
Pteroctopus tetracirrhus (Delle Chiaje, 1830)	115	720	324.9	143.9
Eledone cirrhosa (Lamarck, 1798)	41	660	178.8	122.6
Eledone moschata (Lamark, 1798)	26	366	100.2	65.9
Bathypolypus sponsalis (Fischer and Fischer, 1892)	296	786	561.4	114.1

posed by Field *et al*. (1982), and the strategies suggested were adhered to throughout.

To establish which taxa contributed most to the separation of one group of stations from another, the SIMPER routine was used to compare the mean abundance (number/hour) of each species within each group with that of another group (Clarke, 1993). The contribution of each species to the Bray-Curtis measurement was calculated after root-root transformation and the species were then ranked in two separate groups, percentage and cumulative percentage (Warwick and Clarke, 1991), in order of their contribution. Only the 10 dominant species were considered further.

Physical data (e.g. depth, bottom temperature and bottom type) were collected by various methods. Depth was obtained from the echo-sounder of the vessel, whereas the mean bottom temperatures were recorded using SCANMAR, a gear geometry control mechanism with incorporated temperature sensor. The identification of bottom sediment types was carried out from geological maps of the area studied (Rey and Medialdea, 1989). These data were used to relate physical parameters to the distribution of the cephalopods. The correlation between physical and biotic data was analysed by the HARMONIC correlation coefficient (weighed Spearman coefficient) (Clarke and Ainsworth, 1993).

A variety of different indices was used as measurements of certain community structural attributes. These included: total number of taxa, total number of individuals, species richness: Margalef's index, Shannon-Wiener diversity index, equitability (Pielou's evenness).

Abundance was examined on the basis of station groupings obtained from the dendrogram analyses. In these analyses, the data were not transformed and were grouped by species. The cumulative abundances were illustrated in order of dominance as *k*-dominance curves (Warwick and Clarke, 1991).

Cluster results, dominance curves and between-group comparisons are shown for the MEDITS-ES 96 survey, as a representative example of the results.

RESULTS

In total, 34 species of cephalopods belonging to 11 families were collected (Table 1).

Species assemblages

The 34 species of cephalopods caught in the five cruises were distributed between a depth of 25 and 786 m (Table 1). *Sepiola ligulata*, *Onychoteuthis banksii* and *Chtenopteryx sicula* were caught on a single occasion. *Sepietta obscura*, *Sepiola robusta* and *Sepiola intermedia*, were caught down to 80 m. *Sepietta neglecta*, *Sepia officinalis* and *Octopus vulgaris* were caught down to 200 m. *Heteroteuthis dispar, Histioteuthis bonnellii*, *Histioteuthis reversa*, *Brachioteuthis riisei*, *Bathypolypus sponsalis* and *Opisthoteuthis agassizii* were caught at depths >200 m. The rest of the species showed a wide bathymetric distribution that included the shelf and the beginning of the slope. The widest distributions were represented by *Sepietta oweniana* (27-761 m), *Abralia veranyi* (47-761 m), *Todarodes sagittatus* (87-786 m), *Todaropsis eblanae* (44-693 m), *Eledone cirhosa* (41-660 m) and *Pteroctopus tetracirrhus* (115-720 m).

The dendrogram resulting from the Bray-Curtis analysis of the MEDITS-ES 96 hauls is shown in Figure 2. The principal factor of association was the bathymetric gradient. The first dichotomy separated most of the hauls on the continental shelf and upper edge (1) from the hauls carried out on the middle slope (2). On the continental shelf, the second dichotomy separated the more coastal area of the continental shelf (1.1) from the deep shelf waters and the beginning of the slope (1.2). Within the latter group, hauls 59 (106 m) and 86 (88 m) were an exception

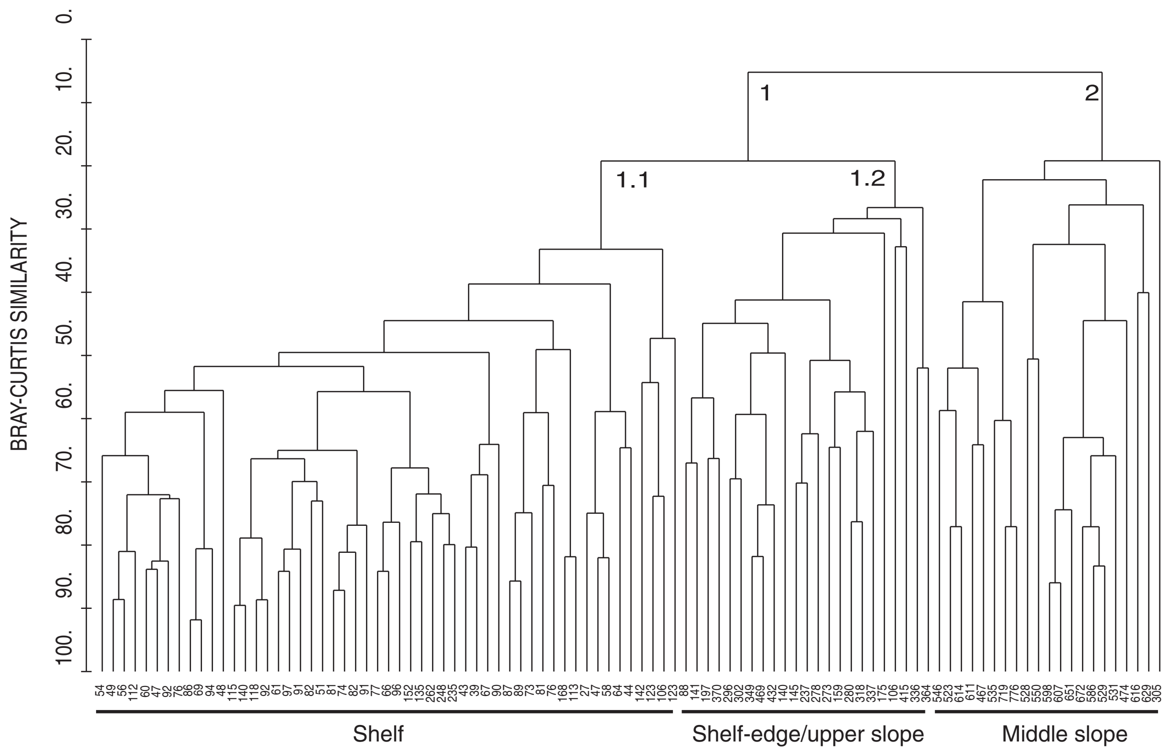

FIG. 2. – Dendrogram showing similarities between hauls based on the composition and abundance of cephalopod species in the MEDITS-ES 96 survey. Mean depth of each haul presented.

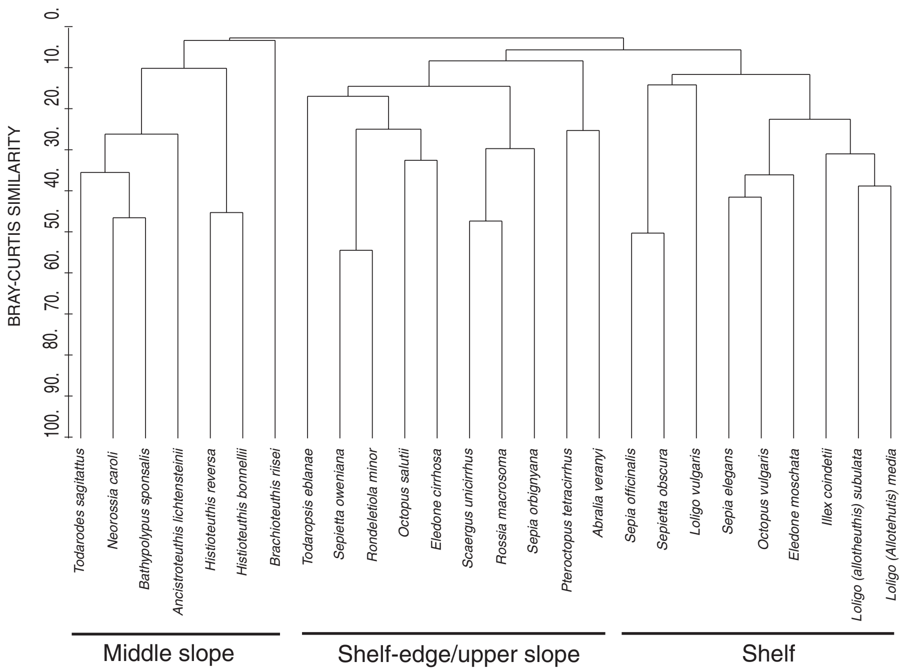

FIG. 3. – Dendrogram of the species relationships from the MEDITS-ES 96 cruise.

due to the combination of two factors: the great abundance of *Eledone cirrhosa* (a species with wide bathymetric distribution found mainly between 100 and 200 m) and the scarce presence of coastal species. The cluster assigned three hauls with depths of approximately 250 m to the shelf group. These hauls should have appeared in the shelf-edge upper slope group since these samples contained species such as *Loligo (Alloteuthis) media* and *Loligo (Alloteuthis) subulata*, which are mainly captured at a depth of 100 m in the MEDITS-ES 96 survey. However, both species are known to occur over a wide depth range from the surface to 350 m (Guerra, 1992).

In the cluster analysis of the species (Fig. 3), the grouping detected agreed with those observed in the samples dendrogram. Three principal clusters illustrated middle slope, shelf-edge upper slope and coastal shelf communities. Middle slope species were the first to be differentiated. This cluster was represented by species caught on the slope such as *Histioteuthis bonnellii*, *Histioteuthis reversa*, *Brachioteuthis riisei*, *Bathypolypus sponsalis, Neorossia caroli* and *Todarodes sagitattus. Sepietta obscura*, *Sepia officinalis, Eledone moschata* and *Octopus vulgaris,* among others, which were included in the shelf group.

Table 2 shows the results of breaking down the dissimilarities between coastal, shelf and slope groups. Species were ordered by their average contribution (average term) to the total average dissimilarity. Indicator species for each group are shown by their high average abundance in the two groups analysed. SIMPER analysis revealed that *Loligo (Alloteuthis) media* was the main indicator species for the coastal shelf group, *Eledone cirrhosa* was the indicator species of the lower shelf-upper slope group, and *Todarodes sagitattus* was the indicator species for the middle slope community. The ratio (i.e. average dissimilarity/SD) indicated which were the most discriminate species. In this case, they coincided with the indicator species for each group: *L. media*, *E. cirrhosa* and *T. sagitattus*. The final column shows the the cumulative percentage of the total dissimilarity that was contributed by each species. Nearly 80% of the contribution to dissimilarity was accounted for by the ten species listed in each comparison, with over 50% accounted for by the first five.

Physical data

The correlation coefficients between the biotic data and abiotic parameters are given in Table 3. Depth was significantly correlated with the cephalopod composition of the hauls on all cruises but not temperature and bottom type. Temperature was stable from around a depth of 100 m (EUROMODEL GROUP, 1995).

TABLE 2. – Between group comparisons, indicator species and related data from the SIMPER analysis of the MEDITS-ES 96 Cruise. Average abundance (Av. ab) contribution of each species to each group. The average term (Av. term) is the average Bray-Curtis contribution of each species to distinguish between groups. The ratio (Av. term/S.D.), the percentage contribution to the separation, and the cumulative percentage is shown for each group comparison. Group 1 is shelf group, group 2 is lower-shelf upper-slope and group 3 is middle slope group.

(a) Shelf v. coastal group. Average dissimilarity: 80.3						
Species	Group 2 Av. ab	Group 1 Av. ab	Av. term	Ratio	%	Cumulative %
Loligo (Alloteuthis) media	0.50	191.84	16.95	1.87	21.10	21.10
Illex coindetii	2.75	22.20	7.87	1.24	9.80	30.91
Loligo (Alloteuthis) subulata	1.42	15.43	7.06	1.12	8.79	39.70
Eledone cirrhosa	10.71	4.55	6.72	1.33	8.37	48.07
Sepietta oweniana	6.25	2.08	6.02	1.18	7.50	55.57
Octopus vulgaris	0.17	3.96	4.54	0.93	5.66	61.23
Rondeletiola minor	5.96	3.24	4.34	0.86	5.40	66.63
Octopus salutii	1.71	0.37	4.06	1.00	5.05	71.68
Todaropsis eblanae	1.04	1.14	3.44	0.82	4.28	75.96
Sepia elegans	0.17	2.86	3.04	0.71	3.78	79.74
(b) Slope v. coastal group. Average dissimilarity: 97.22						
Species	Group 3 Av. ab	Group 1 Av. ab	Av. term	Ratio	%	Cumulative %
Loligo (Alloteuthis) media	0.00	191.84	21.96	2.10	22.58	22.58
Illex coindetii	0.10	22.20	10.44	1.40	10.74	33.32
Loligo (Alloteuthis) subulata	0.00	15.43	8.83	1.14	9.08	42.40
Todarodes sagitattus	1.67	0.08	6.47	1.33	6.65	49.05
Eledone cirrhosa	0.14	4.55	5.74	0.90	5.91	54.96
Octopus vulgaris	0.00	3.96	5.54	0.94	5.70	60.65
Bathypolypus sponsalis	1.29	0.00	4.30	0.87	4.42	65.08
Histioteuthis bonnellii	0.95	0.00	4.15	0.87	4.27	69.34
Sepia elegans	0.00	2.86	3.42	0.66	3.52	72.86
Eledone moschata	0.00	1.08	3.36	0.73	3.45	76.31
(c) Slope v. shelf group. Average dissimilarity: 89.52						
Species	Group 3 Av. ab	Group 2 Av. ab	Av. term	Ratio	%	Cumulative %
Eledone cirrhosa	0.14	10.71	14.48	2.00	16.18	16.18
Sepietta oweniana	0.10	6.25	9.71	1.23	10.85	27.03
Todarodes sagitattus	1.67	0.21	7.45	1.18	8.32	35.35
Octopus salutii	0.57	1.71	6.28	0.99	7.01	42.36
Rondeletiola minor	0.33	5.96	5.93	0.86	6.63	48.99
Bathypolypus sponsalis	1.29	0.21	5.47	0.89	6.11	55.10
Histioteuthis bonnellii	0.95	0.00	5.10	0.85	5.70	60.79
Abralia veranyi	0.57	5.75	4.95	0.69	5.53	66.32
Todaropsis eblanae	0.14	1.04	4.53	0.83	5.06	71.38
Histioteuthis reversa	0.57	0.00	4.04	0.70	4.51	75.89

Ecological indices

In general, there were no significant differences between richness, diversity and equitability (pairwise t-tests) between the different groups formed since the confidence intervals overlapped (Fig. 4). However, certain trends were observed: the taxa number was similar in the shelf and upper-slope and smaller on the middle-slope. The number of individuals decreased with depth, the specific richness was lower on the shelf community than on the upper slope and the middle-slope, the diversity seemed to be greater on the upper slope and the equitability increased with depth.

For the species groups obtained through the BrayCurtis analysis for the 1996 survey it was

TABLE 3. – HARMONIC correlation coefficient (weighed Spearman) between the numerical cephalopod species matrix and physical parameters: depth (D), temperature (T) and bottom type (B); between the numerical cephalopod matrix and pairs of physical parameters: depth-temperature (D-T), depth-bottom type (D-B) and temperature-bottom type (T-B); and between the matrix and all of parameters: depth-temperature-bottom type (D-T-B).

	1994	1995	1996	1997	1998
D	0.601	0.664	0.680	0.702	0.724
T	0.018	0.024	-0.113	0.173	-0.020
B	0.029	-0.045	-0.058	0.014	-0.046
D-T	0.433	0.501	0.412	0.470	0.456
D-B	0.462	0.504	0.426	0.589	0.503
T-B	0.015	-0.019	-0.137	0.061	-0.037
D-T-B	0.349	0.403	0.273	0.421	0.361

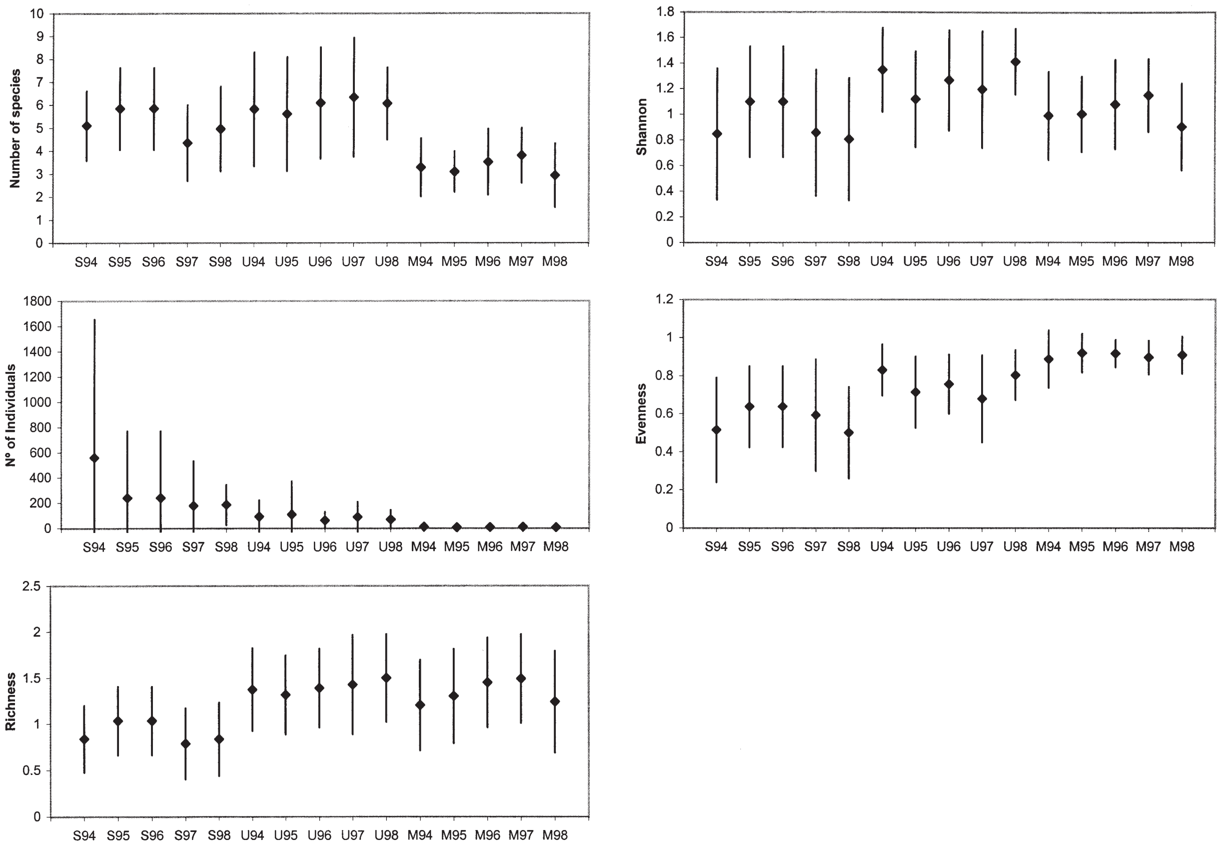

FIG. 4. – Mean and 95% confidence intervals of diversity and evenness indices for each bathymetric community (S = shelf; U = lower shelf upper slope; M = middle slope) and year (1994 – 98).

observed that the diversity was similar for the upper slope and middle slope (Fig. 5). Three species contributed to 50% of the total abundance. In the most coastal community, one single species, *Loligo (Alloteuthis) media*, constituted almost 80% of the abundance. The cumulative abundance curve for this community was high, indicating lower diversity than the other two communities.

DISCUSSION

The 34 cephalopod species distributed in 11 families recorded in this study account for 57.6% of the 59 species reported from the Western Mediterranean (Mangold and Boletzky, 1988). The species not caught were certain species of the Sepiolidae family, pelagic species or species that live at a depth of less than 30 m, or of more than 800 m. In comparison, Tursi and D'Onghia (1992) caught 24 species of cephalopods in the Ionian Sea in 252 hauls between 0 and 650 m, D'Onghia *et al*. (1996) caught 29 species in the North Aegean Sea in 240 hauls between 32 and 490 m, Quetglas *et al*. (2000)

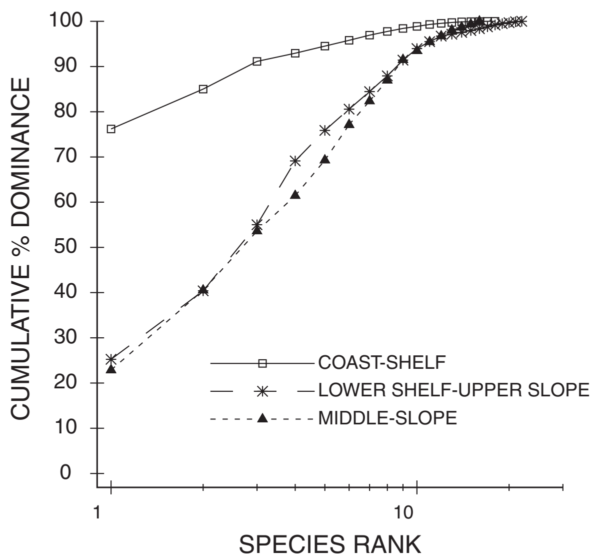

FIG. 5. – Abundance *k*-dominance curves of the principal clusters obtained from the MEDITS-ES 96 survey using untransformed species numerical values.

found 30 species in the Balearic Sea, analysing 79 hauls between 50 and 800 m, and Sánchez *et al*. (1998) found 36 species in the Tyrrhenian Sea and 47 in the Catalan Sea. In this last case, they used additional gear such as plankton nets, and they accumulated data compiled during 20 years of investigation. Except for the monotypic Vampyromorpha, all coleoid orders are represented in the Mediterranean fauna by a total of 19 families out of the 42 described world wide (Mangold and Boletzky, 1988). The number of species found in the different regions of the Mediterranean seems to depend mainly on the sampling effort, the depth range and the types of gears used in the study. D'Onghia *et al*. (1996) considered that the teuthofaunal composition of the North Aegean does not seem less rich than any other Mediterranean basin, such as the northern Ionian Sea and the northern Tyrrhenian Sea.

The spatial distribution of the studied cephalopods is strongly influenced by depth. However, contrary to other studies (Smale *et al*., 1993), there was no influence of temperature and bottom type on this distribution. On the other hand, the type of bottom is a parameter that has a great influence on the spatial distribution of the benthic communities (Demestre *et al*., 2000). Nevertheless, to try to study the relationship between the bottom type and the distribution of the demersal species caught by a trawl haul is complicated, since hauls are usually carried out over soft bottoms, and sometimes a single haul could cross several bottom types, leading to increased difficulty in the analysis.

In general, a similar cephalopod distribution pattern can be observed from the five surveys carried out. In the 1996 survey, the species are divided into three groups: cephalopods on the slope (*Neorossia caroli, Histioteuthis bonnellii*, *Histioteuthis reversa*, *Ancistroteuthis lichtensteinii*, *Todarodes sagittatus*, *Brachioteuthis riisei*, *Bathypolypus sponsalis*), obvious coastal species (*Sepia officinalis*, *Sepia elegans*, *Sepietta obscura*, *Loligo vulgaris, Octopus vulgaris, Eledone moschata)* and a group of species with a wide bathymetric distribution but showing greater abundance on the shelf-edge of the slope (*Sepia orbignyana, Sepietta oweniana*, *Rondeletiola minor*, *Rossia macrosoma, Abralia veranyi, Todaropsis eblanae, Octopus salutii, Scaergus unicirrhus, Pteroctopus tetracirrhus, Eledone cirrhosa*). In studies on the fish community (Massutí *et al*., 1996), and those of other zoological groups (Abelló *et al.* (1988): crustaceans; Smale *et al*. (1993): fish and cephalopods) this distribution pattern is repeated. In other words, the community of the slope is clearly separated from that of the shelf and, within this separation, the species with a narrow bathymetric and coastal range are differentiated from those with a wide distribution. Species belonging to the same families are found in each one of these three communities, thereby indicating a bathymetric diversification within the same family in order to take advantage of the resources and diminish competition (Sánchez *et al.*, 1998). Thus, representatives of the Sepiolidae and Octopodidae families are found in the three bathymetric strata, whereas the Sepiidae and Loliginidae families occur at different depths of the shelf and the Ommastrephidae family appear on the shelf and the slope.

The analysis clearly segregates the slope fauna, but the cephalopods on the shelf are not sufficiently differentiated. This is due to the fact that some species have different distribution patterns depending on which phase of the life cycle they are in. For example, in spring, juvenile *I. coindetii* are found close to the coast (Sánchez, 1986), whereas adults of *L.(Alloteuthis) media* search for shallower waters for spawning, which takes place mainly between March and July (Mangold-Wirtz, 1963). Consequently, species that spend most of their lives in mid-shelf and slope-edge areas can suddenly appear in large quantities in the more coastal strata.

Each association appears to be characterised by an indicator species: *L. (Alloteuthis) media* in the shelf cluster, *E. cirrhosa* in the lower shelf-upper slope cluster and *T. sagitattus* in the middle slope cluster. In the Balearic Sea, the cephalopod community was studied from the point of view of the biomass, which therefore resulted in representative species of *O. vulgaris* for the shelf and *T. sagitattus* for the slope (Quetglas *et al*., 2000). According to the mean abundance (number*h^{-1}), the coastal cluster in the Catalan Sea and the Tyrrhenian Sea was characterized by *Loligo vulgaris*, the continental shelf was characterized by *E. cirrhosa* in the Catalan Sea and *Loligo (Alloteuthis)* sp. in the Tyrrhenian Sea, and the deep-haul group was dominated by the sepiolids (Boletzky, 1995), mainly *Sepietta oweniana* (Sánchez *et al*., 1998). In our study, the number of individuals was very high in the shelf stratum, with richness, diversity and equitability lower than in the other taxocenoses. The dominance curves also reflect a high dominance of one species, *Loligo (Alloteuthis) media*, over the others in the coastal strip. All these indexes are sensitive to the type of net used in the catches, since the diversity decreases with the mesh net size, probably because the small mesh nets retain part of the individuals of the very small species that, in number, are usually dominant (Margalef, 1974). Another factor influencing the distribution of the fauna is the period when the sampling was carried out. Our samples were always collected in spring, while in many other studies the data refer to the whole year.

The assemblage of the lower shelf-upper slope is more diverse and richer in species than the shelf community and the community of the middle slope. Quetglas *et al*. (2000) explained this phenomenon by considering, in their case, the area between a depth of 100 and 600 m as a transitional zone, an area separating different assemblages, that contains overlapping species of two communities, the continental shelf and the slope. Our study supports the existence of a transition area (150-480 m) between the coast and the slope for the cephalopod fauna. This area contains species of wide bathymetric distribution overlapping with species from the two adjacent communities, and some species are present because they are migrating to deeper or shallower depths depending on their life cycle stage (Mangold-Wirz, 1963; Villanueva, 1992).

In addition, species such as *Heteroteuthis dispar*, loliginids, ommastrephids, onychoteuthids, *Histioteuhis* sp., *Abralia veranyi* and *Brachioteuthis riisei* are pelagic cephalopods that carry out vertical daily migrations (Roper and Young, 1975; Villanueva, 1992), remaining close to the bottom during the daytime but distributing themselves in the water column at night.

In conclusion, the spatial distribution of cephalopods may depend on a large combination of physical factors (e.g. depth, temperature and bottom type) and biological factors (e.g. ontogenetic migrations, daily vertical migrations and the relationships between species). The distribution observed is possibly the result of the interaction of these factors.

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